

Epiphytic bryophyte communities of *Prunus lusitanica* Iberian forests: biogeographic islands shaped by regional climates

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Abstract – Epiphytic communities of Iberian forests remain partly unknown and most studies have focused on the dominant oak forests. We provide a comprehensive analysis and interpretation of the epiphytic bryophyte communities of forests dominated by the Tertiary relict evergreen cherry *Prunus lusitanica*. This type of forest, scattered in the western and northern half of the Iberian Peninsula, harbours a noticeable richness of epiphytic bryophytes, including an outstanding number of liverwort species. Their floristic composition varies markedly across the Peninsula yet is driven by the main climate patterns prevailing in the area. Multivariate analyses (TWINSPAN, CCA) render two main groups of epiphytic communities with their respective indicator species. Both groups share a high proportion of non-Mediterranean species, a circumstance that is most remarkable in the forests that fall within the Mediterranean Region, which could be considered as ecological refuges or biogeographic islands.

Bryoflora / biogeographic elements / distribution / biodiversity / epiphytes / Iberian Peninsula / liverworts / mosses / species richness

INTRODUCTION

The Iberian Peninsula harbours an outstanding diversity of forests with a large variety of vascular floristic assemblages extensively described (Peinado Lorca & Rivas-Martínez, 1987; Rivas-Martínez, 1987a, 2006, 2007, 2011a, 2011b; Costa-Tenorio *et al.*, 1997; Sainz Ollero & Sánchez de Dios, 2011). In recent decades, the epiphytic bryophyte communities of Iberian forests have also been studied but these investigations have focused mainly on oak (*Quercus* sp. pl.) forests (Gil & Guerra, 1981, 1985; Burgaz *et al.*, 1994a, 1994b; Lara & Mazimpaka, 1994, 1998; Mazimpaka & Lara, 1995; Albertos *et al.*, 2005; Garcia *et al.*, 2004, 2005; Marques *et al.*, 2005; Garcia, 2006; Mazimpaka *et al.*, 2009; Medina *et al.*, 2015). To a lesser extent, other singular forests that have been studied include those dominated by *Juniperus thurifera* L. (Medina *et al.*, 2010), *Olea europaea* L. (Sim-Sim *et al.*, 1995), *Rhododendron ponticum* subsp. *baeticum* (Boiss. & Reut.) Hand.-Mazz. (Gil &

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Guerra, 1981; Guerra *et al.*, 2003), *Abies pinsapo* Boiss. (Guerra, 1982) and *Prunus lusitanica* L. (Albertos *et al.*, 1997; Calleja *et al.*, 2001).

The richness and composition variability of the epiphytic bryoflora of the Iberian forests have been analysed throughout altitudinal gradients, tree microhabitats and trunk dimensions (Mazimpaka & Lara, 1995; Lara & Mazimpaka, 1998; Mazimpaka *et al.*, 2009; Medina *et al.*, 2014), across bioclimatic boundaries (Albertos *et al.*, 2005; Medina *et al.*, 2014) and at large geographic scales (Burgaz *et al.*, 1994a, 1994b; Lara, 1993; Fuertes *et al.*, 1996; Medina *et al.*, 2010). Both regional and local factors shape the variability of epiphytic bryophyte assemblages (Burgaz *et al.*, 1994a; Mazimpaka & Lara, 1995; Fuertes *et al.*, 1996; Lara & Mazimpaka, 1998; Mazimpaka *et al.*, 2009; Medina *et al.*, 2010; Medina *et al.*, 2014). At the regional scale, climate seems to be the main driver of the diversity and composition of epiphytic bryophyte communities (García, 2006; Medina *et al.*, 2010; Medina *et al.*, 2014). At a local scale, microclimatic conditions plus historical factors may also favour unexpected epiphytic bryophytes that reveal singular biogeographic islands within forests inhabiting Mediterranean environments. Thus, the Iberian relict forests of *Rhododendron ponticum*, close to the Strait of Gibraltar, host Macaronesian species (Gil & Guerra, 1981; Guerra *et al.*, 2003). Likewise, forests of *Quercus ilex* subsp. *ballota* (Desf.) Samp. in Sierra Alhamilla, a southeastern Iberian mountain nestled in the driest zone of Europe (Mazimpaka *et al.*, 2009), support rich communities with an unpredicted proportion of mesic species.

Among the Iberian forests, those dominated by *Prunus lusitanica* stand out, as it is a relict evergreen broadleaved cherry tree related to the Tertiary flora (Pignatti, 1978; Barrón *et al.*, 2010). *Prunus lusitanica* groves occur in the western and northern halves of the Iberian Peninsula (Calleja & Sainz, 2009), within two very different biogeographical and climatic regions: the Mediterranean and Eurosiberian Regions (Rivas-Martínez, 1987a; Costa-Tenorio *et al.*, 1997; Sainz Ollero & Sánchez de Dios, 2011). They usually colonise exceptionally wet sites, mainly on riverbanks and around springs in deep gullies and valleys, situated at middle altitudes in mountainous regions (Calleja *et al.*, 2009; Garilleti *et al.*, 2012). The very specific environmental preferences of *P. lusitanica* might be expected to promote homogeneous epiphytic bryophyte communities irrespective of the regional climates, since these organisms are very sensitive to microclimates (Barkman, 1958; Vanderpoorten *et al.*, 2004; Raabe *et al.*, 2010). Furthermore, the microclimatic conditions preferred by this subtropical relict species may also favour the presence of Macaronesian epiphytic bryophytes, as registered in *Rhododendron ponticum* stands (Gil & Guerra, 1981; Guerra *et al.*, 2003). Results of a preliminary study based on a limited number of forests surveyed (Calleja *et al.*, 2001) do not fully support these hypotheses. However, several local studies of the bryoflora inhabiting Iberian *P. lusitanica* forests remark the occurrence of singular bryophytes within the Mediterranean Region (Albertos *et al.*, 1997; Casas *et al.*, 1999; Sérgio *et al.*, 2001). To date, we have a fragmentary knowledge of the floristic richness and composition variability of the epiphytic bryoflora of *P. lusitanica* forests across the Iberian Peninsula, and we ignore the environmental drivers of composition changes in these communities.

The present study focus on epiphytic bryophytes inhabiting the trunks (excluding tree bases and branches) of *Prunus lusitanica* forests and our major aims are to i) provide a comprehensive perspective on the richness and variability of these communities throughout the Iberian Peninsula; ii) confirm whether these forests act as biogeographic islands, hosting unexpected species in different geographical and regional climate contexts; and iii) evaluate the potential relationship between regional climates and the floristic variability of the epiphytic bryophyte communities of this type of forests.

MATERIALS AND METHODS

We studied the epiphytic bryoflora growing on the trunks of 14 forests dominated or co-dominated by *Prunus lusitanica*, which encompass all the main nuclei of distribution of this type of forest in the Iberian Peninsula. Sampled forests were selected based on their optimal structure and representativeness (Calleja & Sainz, 2009) and severely disturbed forests or those with less than 25 individuals were discarded. In those areas where *P. lusitanica* becomes fairly common (Calleja *et al.*, 2009), two well preserved forests have been selected. Study sites are located in nine geographic areas within two different biogeographical regions, the Mediterranean and Eurosiberian (Tables 1, 2 and 3, Fig. 1). The boundaries and definition of both biogeographical regions follow the climatic and floristic criteria described by several authors (Rivas-Martínez, 1987a, 1987b; Moreno *et al.*, 1990;

Table 1. Geographical information of studied *Prunus lusitanica* forests. Country: PT = Portugal and SP = SPAIN; Provinces: AV = Ávila, BB = Beira Baixa, BL = Beira Litoral, BU = Burgos, CC = Cáceres, CR = Ciudad Real, GE = Gerona, LE = León, MH = Minho, NA = Navarra, and TO = Toledo; No. of trees = number of trees sampled

N.	Population	Geographical region	Country	Province	Locality	Coordinates (WGS84)	No. of trees
1	MTo1	Montes de Toledo	SP	CR	Arroyo del Robledillo	04° 31' 21.99" W 39° 25' 26.91" N	25
2	MTo2	Montes de Toledo	SP	TO	Garganta Las Lanchas	04° 53' 20.21" W 39° 34' 25.96" N	22
3	LVi1	Las Villuercas	SP	CC	La Trucha	05° 14' 57.41" W 39° 32' 52.03" N	23
4	LVi2	Las Villuercas	SP	CC	Apretura río Viejas	05° 27' 26.27" W 39° 36' 29.98" N	24
5	Gre1	Sierra de Gredos	SP	AV	Río Muelas	05° 11' 24.17" W 40° 10' 40.03" N	22
6	Gre2	Sierra de Gredos	SP	AV	Garganta Santa María	05° 13' 57.53" W 40° 11' 59.08" N	18
7	Aço1	Sierras de Açor	PT	BB	Río Ceira	07° 51' 09.90" W 40° 10' 37.74" N	25
8	Aço2	Sierras de Açor	PT	BL	Mata da Margaraça	07° 55' 10.07" W 40° 12' 56.83" N	20
9	Mon1	Montseny-Guilleries	SP	GE	Sot de l'Escala	02° 29' 48.5" E 41° 46' 30.8" N	25
10	Mon2	Montseny-Guilleries	SP	GE	Sant Pere Desplà	02° 28' 43.85" E 41° 50' 38.69" N	25
11	Anca	Sierra de Ancares	SP	LE	Río Fresnedelo	06° 37' 39.64" W 42° 48' 56.8" N	20
12	Gere	Sierra de Gêres	PT	MH	Río Home	08° 08' 57.49" W 41° 47' 22.38" N	18
13	CCan	Sierra de Ordunte	SP	BU	Arroyo del Lloral	03° 18' 26.61" W 43° 09' 40.4" N	25
14	POcc	Pirineo Occidental	SP	NA	Río Urrizate	01° 23' 29.95" W 43° 15' 12.85" N	18

Table 2. Biogeographical regions, climatic characterisation and brief vegetation description of studied sites. Alt. = Altitude; Climatic characterisation following Font Tullot (1983); Biogeog. region = Biogeographical region: Med = Mediterranean, Eur = Eurosiberian, Med / Eur = transitional between both regions; Dominant vegetation, Z = Zonal vegetation, Az = Azonal vegetation

<i>Population</i>	<i>Alt (m)</i>	<i>Climatic characterization</i>	<i>Biogeog. region</i>	<i>Dominant vegetation</i>
MT01	700	Mediterranean and continental	Med	Z: forests of <i>Quercus faginea</i> subsp. <i>broteroi</i> , <i>Q. ilex</i> subsp. <i>ballota</i> and <i>Q. suber</i> ; Az: dense patches of <i>Prunus lusitanica</i> mixed with <i>Betula pendula</i> , <i>Fraxinus angustifolia</i> and <i>Salix atrocinerea</i>
MT02	900	Mediterranean and continental	Med	Z: forests of <i>Quercus pyrenaica</i> ; Az: small forest of <i>Prunus lusitanica</i> with <i>Betula pendula</i> and <i>Taxus baccata</i>
LVi1	620	Mediterranean and continental	Med	Z: forests of <i>Quercus pyrenaica</i> ; Az: forests of <i>Alnus glutinosa</i> and <i>Prunus lusitanica</i>
LVi2	500	Mediterranean and continental	Med	Z: forests of <i>Quercus faginea</i> subsp. <i>broteroi</i> and <i>Q. suber</i> ; Az: forests of <i>Alnus glutinosa</i> and <i>Prunus lusitanica</i>
Gre1	660	Mediterranean and attenuated continental	Med	Z: forests of <i>Quercus pyrenaica</i> ; Az: forests of <i>Alnus glutinosa</i> and a dense patch of <i>Prunus lusitanica</i>
Gre2	630	Mediterranean and attenuated continental	Med	Z: forests of <i>Quercus pyrenaica</i> . Az: dense patch of <i>Prunus lusitanica</i>
Aço1	600	Mediterranean and Atlantic	Med	Z: burned forests of <i>Arbutus unedo</i> and <i>Pinus pinaster</i> and <i>Quercus</i> sp. pl.; Az: dense patches of <i>Prunus lusitanica</i>
Aço2	625	Mediterranean and Atlantic	Med	Z: mixed forests of <i>Castanea sativa</i> and <i>Quercus robur</i> ; Az: mixed forest of <i>Corylus avellana</i> , <i>Prunus lusitanica</i> and <i>Salix atrocinerea</i>
Mon1	760	Northeastern Mediterranean	Med / Eur	Z: forests of <i>Fagus sylvatica</i> and <i>Quercus ilex</i> subsp. <i>ilex</i> ; Az: mixed forests of <i>Corylus avellana</i> , <i>Fagus sylvatica</i> , <i>Ilex aquifolium</i> , <i>Prunus lusitanica</i> and <i>Salix atrocinerea</i>
Mon2	550	Northeastern Mediterranean	Med / Eur	Z: forests of <i>Quercus suber</i> ; Az: mixed forests of <i>Alnus glutinosa</i> , <i>Corylus avellana</i> , <i>Fraxinus excelsior</i> and <i>Prunus lusitanica</i>
Anca	740	Western and semi-maritime European	Med / Eur	Z: forests of <i>Quercus pyrenaica</i> and <i>Q. robur</i> ; Az: forests of <i>Alnus glutinosa</i> and dense patches of <i>Prunus lusitanica</i>
Gere	720	Western and maritime European	Eur	Z: forests of <i>Quercus robur</i> ; Az: riparian forests of <i>Alnus glutinosa</i> and patches of <i>Prunus lusitanica</i>
CCan	500	Western and maritime European	Eur	Z: forests of <i>Fagus sylvatica</i> , <i>Quercus pyrenaica</i> and <i>Q. robur</i> ; Az: mixed forests of <i>Corylus avellana</i> , <i>Frangula alnus</i> and <i>Prunus lusitanica</i>
POcc	175	Western and semi-maritime European	Eur	Z: forests of <i>Fagus sylvatica</i> ; Az: riparian forest of <i>Corylus avellana</i> , <i>Fraxinus excelsior</i> and <i>Prunus lusitanica</i>

Table 3. Epiphytic bryophytes collected on trunks of 14 *Prunus lusitanica* forests. Species abbreviations (Abbrev.), phylogeographical characterisation (Phyto geography), Index of Ecological Significance (IES) values, and number of localities (No. loc.) are shown for each species. Species abbreviations combine the first three letters of the generic name and the first two of the specific name. Phylogeographical elements abbreviations: Eur = Eurosiberian, Eur-Oce = Eurosiberian and Oceanic, Ind = Indifferent, Med = Mediterranean, Med-Oce = Mediterranean and Oceanic, Oce = Oceanic

Species	Abbrev.	Phyto geography	IES values														No. loc.	
			MTo1	MTo2	Lf1	Lf2	Gre1	Gre2	Aç1	Aç2	Mon1	Mon2	Anca	Gere	CCan	POcc		
<i>Alleniella complanata</i>	ALL CO	Eur-Oce	-	-	-	8.3	6.8	-	-	13.0	102.5	48.1	240.0	7.5	16.7	72.0	-	9
<i>Anitrichia californica</i>	ANT CA	Med	-	-	6.5	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Anitrichia curtipendula</i>	ANT CU	Eur	-	-	-	-	-	-	-	-	-	-	-	-	16.7	-	-	1
<i>Brachythecium dieckii</i>	BRA DI	Med-Oce	-	-	6.5	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Brachythecium velutinum</i>	BRA VE	Oce	-	-	6.5	6.3	-	-	-	15.0	-	102.0	7.5	-	38.0	-	6	
<i>Cololejeunea minutissima</i>	COL MI	Oce	-	-	-	-	-	-	-	38.9	-	11.1	-	-	30.6	-	3	
<i>Cololejeunea rossettiana</i>	COL RO	Oce	-	-	-	-	-	-	-	-	-	56.0	-	-	-	-	1	
<i>Cryphaea heteromalla</i>	CRY HE	Oce	-	-	-	-	95.5	-	7.4	10.0	-	8.0	-	-	-	-	4	
<i>Dicranella heteromalla</i>	DIC HE	Eur-Oce	-	-	-	-	-	-	-	-	-	-	-	7.5	-	-	1	
<i>Dicranoweisia cirrata</i>	DIC CI	Oce	-	-	-	-	-	-	-	-	-	-	-	15.0	-	-	1	
<i>Dicranum scoparium</i>	DIC SC	Eur	-	-	-	-	-	-	-	-	-	-	-	7.5	19.4	-	2	
<i>Eurhynchium</i> sp.	EUR	-	-	-	-	-	-	-	-	-	-	-	6.0	-	-	-	1	
<i>Fabronia pusilla</i>	FAB PU	Med-Oce	-	-	-	-	25.0	-	-	-	-	-	-	-	-	-	1	
<i>Frullania dilatata</i>	FRU DI	Oce	384.0	245.5	282.6	295.8	150.0	80.6	357.4	252.5	440.7	100.0	95.0	61.1	262.0	238.9	14	
<i>Frullania fragilifolia</i>	FRU FR	Eur-Oce	-	-	-	-	-	-	-	-	-	-	-	62.5	-	126.0	11.1	3
<i>Frullania microphylla</i>	FRU MI	Eur-Oce	-	-	-	-	-	-	-	-	-	-	-	17.5	-	-	44.4	2
<i>Frullania oakesiana</i>	FRU OA	Oce	-	-	-	-	-	-	-	-	-	-	-	-	-	14.0	-	1

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Species	Abbrev.	Phyto geography	IES values													No. loc.	
			MTo1	MTo2	LVi1	LVi2	Gre1	Gre2	Açol	Aço2	Mon1	Mon2	Anca	Gene	CCan		POcc
<i>Orthotrichum affine</i>	ORT AF	Ind	48.0	-	-	-	-	-	-	5.6	8.0	-	-	-	-	-	3
<i>Orthotrichum ibericum</i>	ORT IB	Med-Oce	-	-	-	-	-	-	5.6	-	-	-	-	-	-	-	1
<i>Orthotrichum lyellii</i>	ORT LY	Oce	184.0	115.9	130.4	29.2	93.2	138.9	83.3	40.0	5.6	12.0	-	33.3	158.0	55.6	13
<i>Orthotrichum pallens</i>	ORT PA	Eur	-	-	-	8.3	-	-	-	-	-	-	-	-	-	-	1
<i>Orthotrichum pumilum</i>	ORT PU	Med	-	-	-	-	-	-	-	-	14.0	-	-	-	-	-	1
<i>Orthotrichum rupestre</i>	ORT RU	Med	-	111.4	-	-	31.8	27.8	-	-	-	-	-	8.3	-	-	4
<i>Orthotrichum spectosum</i>	ORT SP	Eur	8.0	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Orthotrichum striatum</i>	ORT ST	Oce	42.0	15.9	30.4	-	56.8	11.1	38.9	-	-	-	-	-	-	-	6
<i>Orthotrichum tenellum</i>	ORT TE	Med-Oce	150.0	38.6	54.3	22.9	6.8	-	38.9	-	6.0	-	-	-	-	-	7
<i>Porella obtusata</i>	POR OB	Oce	-	102.3	-	14.6	15.9	-	-	7.5	6.0	-	152.8	-	-	-	6
<i>Pterigandrum filiforme</i>	PTE FI	Eur	-	-	-	-	-	-	-	-	-	-	7.5	11.1	-	-	2
<i>Radula complanata</i>	RAD CO	Eur	-	22.7	13.0	72.9	79.5	127.8	144.4	170.0	246.3	298.0	15.0	125.0	58.0	-	12
<i>Rhynchostegium confertum</i>	RHY CO	Ind	-	-	-	-	-	-	-	-	-	12.0	-	-	-	-	1
<i>Syntrichia laevipila</i>	SYN LA	Med-Oce	6.0	-	6.5	-	-	-	-	-	-	-	-	-	-	-	2
<i>Ulota bruchii</i>	ULO BR	Eur	-	-	-	-	-	-	-	-	-	-	-	42.0	19.4	2	
<i>Ulota crispa</i>	ULO CR	Eur	-	-	-	-	-	-	-	-	-	-	-	30.0	22.2	2	
<i>Ulota crispula</i>	ULO CL	Eur	-	-	-	-	-	-	-	-	-	-	-	30.0	80.6	2	
<i>Zygodon rupestris</i>	ZYG RU	Med-Oce	-	-	6.5	-	6.8	-	22.2	55.0	5.6	18.0	7.5	11.1	24.0	-	9

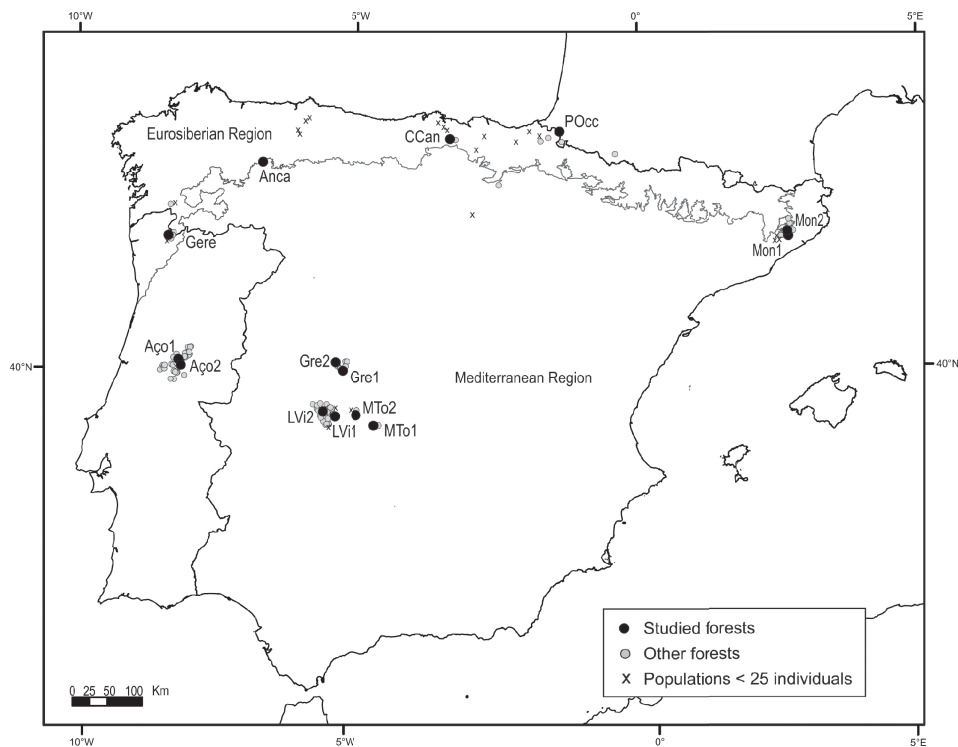


Fig. 1. *Prunus lusitanica* distribution (light grey dots) and locations of the studied forests (black dots). “X” indicates localities with less than 25 individuals of *P. lusitanica*. The grey line marks the boundary between the Eurosiberian and Mediterranean Regions as drawn by Rivas-Martínez (1987b). Studied forest abbreviations are shown in Table 1.

Costa-Tenorio *et al.*, 1997). Thus, eight forests are located in the Mediterranean Region (symbolised as MTo1, MTo2, LVi1, LVi2, Gre1, Gre2, Aço1, Aço2), three forests are located within the Eurosiberian Region (Gere, CCan, POcc), and three more occur close to the boundaries of these two regions (Mon1, Mon2, Anca).

In each forest, 18–25 trunks of *P. lusitanica* were randomly sampled. Very thin stems (<5 cm of diameter) or bent ones (>25°) were discarded. Bryophytes were sampled on each trunk within a 400 cm² plot, set at a height between 1.3 and 1.5 m above ground level, avoiding braches and tree bases. This delimitation was further maintained for comparison of richness values and floristic assemblages, so that when using bibliographic sources only data corresponding to trunks were considered. This is based on the fact that in our latitudes trunks (1 m above ground level) and bases of a given phorophyte hold different epiphytic communities (Lara, 1993; Mazimpaka & Lara, 1995). Additionally, the bark of trunks is a xeric environment (Barkman, 1958; Mazimpaka & Lara, 1995) that maximises the interrelationship between the epiphytic bryoflora and the prevailing climates (Barkman, 1958; Medina *et al.*, 2014). All plots were set on the trunk side with the highest bryophyte cover and the total bryophyte cover per plot was noted before removal of the sample, so that species cover estimated in the laboratory could be related to that in the field (Albertos *et al.*, 2005). Both cover estimates were obtained with the aid of a graphic chart (William, 1986).

For composition analysis purposes, all identified bryophyte species were assigned to one of six phytogeographical elements, considering their global distribution and their abundances as epiphytic species within the Iberian Peninsula. The phytogeographical spectrum per forest was obtained by calculating the percentage of species grouped within each element. The phytogeographical elements are: the Eurosiberian element (Eur), comprising species living primarily and widely distributed in the Eurosiberian Region; the Mediterranean element (Med), comprising species with their main distribution in Mediterranean territories with typical summer droughts; the Oceanic element (Oce), comprising species growing in both regions under mild climatic conditions taking advantage of the buffer influence of the sea or orographic rainfalls; the Eurosiberian-Oceanic element (Eur-Oce), comprising species living in Eurosiberian territories where cold winters are buffered by the proximity of the Atlantic Ocean; the Mediterranean-Oceanic element (Med-Oce), comprising species with their main distribution in Mediterranean zones where summer droughts or/and the continentality are buffered by the humidity provided either by the sea (Mediterranean Sea or Atlantic Ocean) or by orographic rainfalls; and the Indifferent element (Ind), comprising species with their main distribution unrelated to the above climate patterns. This classification (Appendix 1) is based on: i) chorological information from a compilation of the Iberian records of epiphytic bryophytes (CORIA, as described in Albertos, 2001), complemented with that available in *Flora Briofítica Ibérica* (Guerra & Cros, 2006-2014), *Cartografía de Briofitas. Península Ibérica i Illes Balears* (<http://briofits.iec.cat>) and GBIF (<http://www.gbif.org>); and ii) phytogeographical classifications provided by Düll (1983, 1984, 1985, 1992), Hill and Preston (1998), and Albertos (2001), complemented with those of Dierssen (2001) and Bischler (2004). The Iberian climatic division follows the scheme of Font Tullot (1983).

The epiphytic bryophyte diversity of each forest was calculated using the Shannon-Weaver index (Shannon & Weaver, 1963): $H' = -\sum_{i=1}^s p_i \ln p_i$, where “ p_i ” refers to the frequency of each “ i ” species per forest, *i.e.* the proportion of trunks where each “ i ” species has been found regarding the total number of sampled trunks of each forest. Independently, the abundances of each species per forest were calculated using the Index of Ecological Significance (IES), which combines both frequency and cover (Lara & Mazimpaka, 1998; Albertos *et al.*, 2001; Mazimpaka *et al.*, 2009). IES values were also used for two multivariate analyses: a classification analysis with indicator species (TWINSPAN) using the Community Analysis Package software (Seaby *et al.*, 2004), and a canonical correspondence analysis (CCA) using the statistical package Canoco for Windows 4.5 (Ter Braak & Prentice, 1988; Ter Braak & Smilauer, 2002). TWINSPAN analysis is a powerful tool that provides species and their abundance levels (pseudospecies) responsible for classification dichotomies, *i.e.* forest groups in our study (Hill, 1979). Four pseudospecies have been considered, based on meaningful levels of IES values: 1- IES = 1–50 (scarce); 2- IES = 51–150 (common), 3- IES = 151–250 (abundant), and 4- IES > 250 (dominant). For each dichotomy, the classification rendered indicators and preferential pseudospecies (Leps & Smilauer, 2003). For simplicity, only indicator pseudospecies were graphically represented along with those preferential ones occurring in more than 80% of the samples of a given dichotomy. The complete data of the TWINSPAN analysis are available in Appendix 2.

The CCA involved two complementary matrices: i) a taxa matrix ($n = 53$) with their corresponding IES values for each studied forest ($n = 14$); ii) a matrix with the following environmental variables ($n = 12$) for the same forests: altitude (Alt); Continentality Index of Gorezyski (K), following Aguiló Alonso *et al.* (1995);

mean annual rainfall (P); mean summer rainfall from June to August (P_{sum}); distance from each forest to the sea (D); mean annual temperature (T); mean summer temperature from June to August (T_{sum}); mean maximum temperature of the hottest month (T_{max}); mean minimum temperature of the coldest month (T_{min}); mean temperature range (T_{range}); annual potential evapotranspiration (Th) calculated as Thornthwaite's index (Aguiló Alonso *et al.* 1995); potential evapotranspiration in summer, from June to August (Th_{sum}). Data were taken from the online WorldClim database (<http://www.worldclim.org/>, version 1.4) and the Iberian Climate Atlas (A.E.M.E.T & I.M.I.P, 2011). To obtain a simple and statistically significant model, a selection process of the 12 environmental variables was performed using the Canoco for Windows 4.5 statistical package (Ter Braak & Prentice, 1988; Ter Braak & Smilauer, 2002). Autocorrelated variables with high inflation scores (VIF values > 1.5) were discarded and the significance of the resulting model was tested by a Monte Carlo test with permutations (Ter Braak & Smilauer, 2002). To complete the explanation of community variability, the IES values of the six above-mentioned phytogeographical elements per forest were projected as supplementary variables in the final model (without affecting its eigenvalues and statistical significance) (Ter Braak & Smilauer, 2002; Leps & Smilauer, 2003). Both environmental and phytogeographical data per forest are available in Appendix 3, and CCA data analysis are provided in Appendix 4.

Taxon nomenclature follows Ros *et al.* (2007) for liverworts and Ros *et al.* (2013) for mosses, except for the genus *Ulota* D.Mohr that follows Caparrós *et al.* (2014). Flora Ibérica (Castroviejo, 1986-2014) was used for vascular plants.

RESULTS

Richness and diversity

The epiphyte bryoflora on trunks of the 14 sampled *Prunus lusitanica* forests comprises 53 species: 41 mosses and 12 liverworts (Table 3 and Fig. 2). The family Orthotrichaceae is especially well represented with 3 genera and 15 species. In addition, the families Brachytheciaceae, Frullaniaceae and Lejeuneaceae are represented by 1 to 5 genera with 5 species per family. *Frullania* Raddi among liverworts and *Orthotrichum* Hedw. among mosses are the most species-rich genera, with 5 and 11 species respectively (Table 3).

Three liverworts: *Frullania dilatata* (L.) Dumort., *Metzgeria furcata* (L.) Dumort., and *Radula complanata* (L.) Dumort., and two mosses: *Hypnum cupressiforme* Hedw. and *Orthotrichum byellii* Hook. & Taylor, occur in nearly all the sampled forests. In contrast, 29 species are found in fewer than three forests (Table 3).

Richness per forest varies from 11 to 20 species (mean = 16.4 ± 3.2), the number of moss species per forest usually being greater than that of liverworts. Similar richness figures are found in Mediterranean and Eurosiberian forests (including those in transitional areas), 16.0 ± 3.3 and 17.0 ± 3.2 , respectively. The number of liverworts is slightly higher in Eurosiberian and transitional forests (range = 6–8, mean = 6.7 ± 0.8) than in the Mediterranean ones (range = 2–6, mean = 4.0 ± 1.2) (Fig. 2), yet some liverworts (*Frullania dilatata*, *Metzgeria furcata* and *Radula complanata*) show high IES values in the latter region (Table 3).

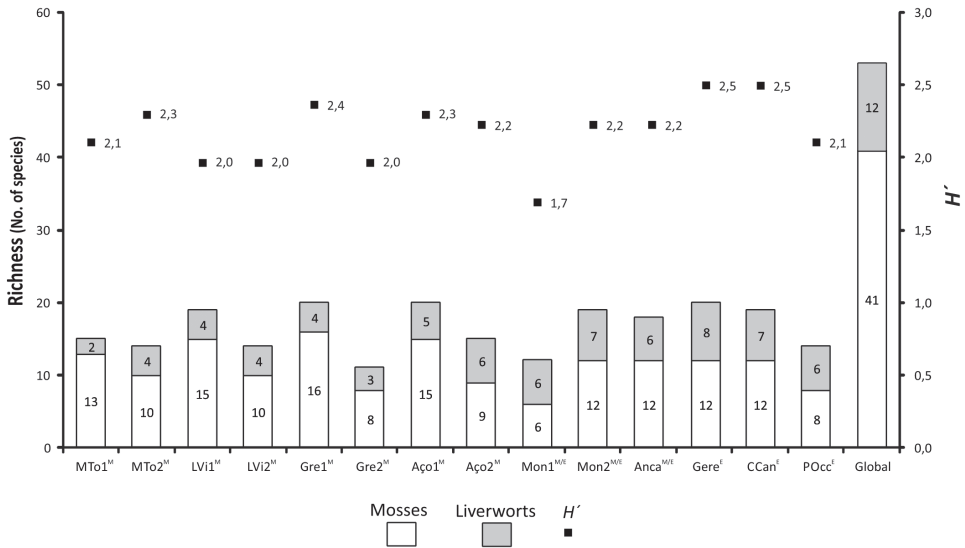


Fig. 2. Richness of mosses and liverworts and Shannon-Weaver diversity index (H') of the 14 *Prunus lusitanica* forests. Population abbreviations are shown in Table 1. Superscript letters on forest abbreviations refer to the biogeographical regions: M = Mediterranean Region, E = Eurosiberian Region, M/E = transitional between both regions.

The Shannon-Weaver index (H') varies from 2 to 2.5 in most forests, forest Mon1 being the exception, with a value of only 1.7 (Fig. 2).

Phytogeographical spectra

Heterogeneity in bryophyte composition affects not only the identity of the species involved but also the phytogeographical spectra of each forest. This is true even for groves located in the same biogeographical region and geographical area (Figs. 1 and 3). Despite this variability, some general trends arise. The Oceanic element shows high percentages in all the surveyed forests (21-40%). The Mediterranean element never dominates, even in forests located within the Mediterranean Region, where it can occasionally be absent. This Mediterranean element is also poorly represented or totally absent in most of the forests located in the Eurosiberian Region or in its boundaries. Likewise, the Mediterranean-Oceanic element shows low percentages in these forests. Instead, the Eurosiberian and Eurosiberian-Oceanic elements gain great relevance in the communities of forests growing in the Eurosiberian Region. This last result also applies, although with more modest values, in the westernmost (Est1 and Est2) and northeastern (Mon1) communities of the Mediterranean Region.

Classification analysis TWINSpan

Certain indicator and preferential pseudospecies (species at different abundance levels) discriminate different epiphytic bryophyte communities growing on trunks of *Prunus lusitanica* forests, with eigenvalues ranging from 0.29 to

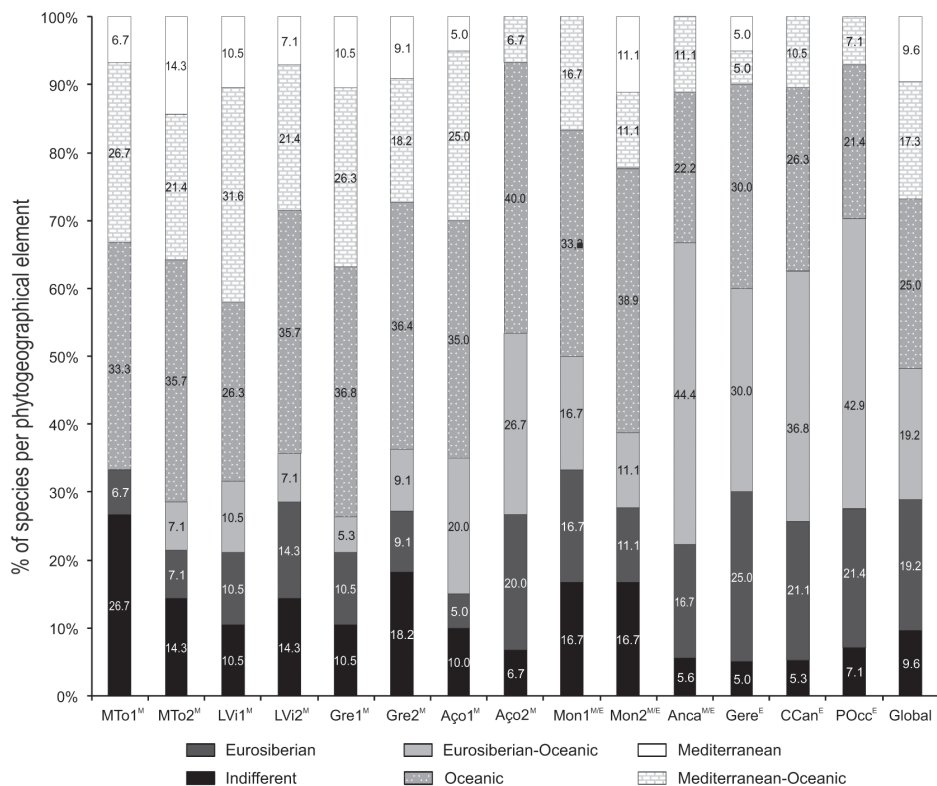


Fig. 3. Phytogeographical spectrum of epiphytic communities of the 14 forests of *Prunus lusitanica*. The numbers of species per phytogeographical element are represented as percentages. Superscript letters on forest abbreviations refer to the biogeographical regions: M = Mediterranean Region, E = Eurosiberian Region, M/E = transitional between both regions.

0.41 (Fig. 4). Half of the communities (dendrogram branches with letter *a*) share the Eurosiberian-Oceanic liverwort *Frullania tamarisci* (L.) Dumort. These communities occur in only one forest located in the Mediterranean Region (Aço2), in all the three forests growing in the boundary of both biogeographical regions (Mon1, Mon2 and Anca) and in all the forests of the Eurosiberian Region (Gere, CCan and POcc) (Figs. 1 and 4). Four subgroups are discriminated: i) Mon1 y Mon2 forests, with communities mainly distinguished by the presence of *Orthotrichum affine* Schrad. ex Brid. and the absence of *Isothecium myosuroides* Brid. and *Neckera pumila* Hedw.; ii) Gere and Aço2 forests host communities discriminated by *Porella obtusata* (Taylor) Trevis and *Lejeunea cavifolia* (Ehrh.) Lindb. with noticeable abundance of *I. myosuroides* along with the lack of *Frullania fragilifolia* (Taylor) Gottsche, Lindenb. & Nees and *Hypnum cupressiforme*; iii) CCan and POcc forests support communities characterised by *F. fragilifolia* and the noticeable abundance of *H. cupressiforme* and segregated from the next clade by the presence of *Leptodon smithii* (Hedw.) F. Weber & D. Mohr, *Microlejeunea ulicina* (Taylor) A. Evans, and *Ulota sp. pl.*; iv) the community of Anca forest diverges from “group iii” (CCan and

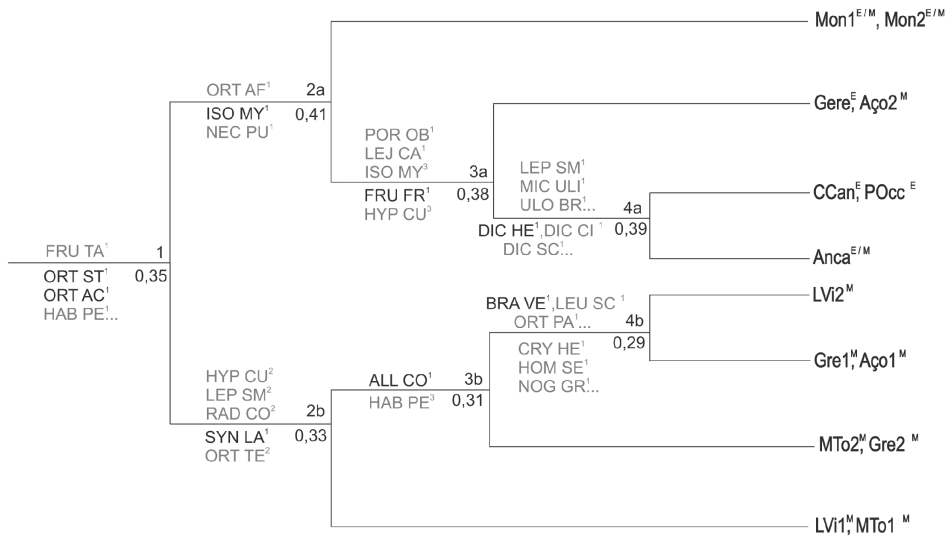


Fig. 4. TWINSpan classification of *Prunus lusitanica* forests. Correspondence between abbreviations and full names of forests and species are provided in Tables 1 and 3. Each dichotomy is identified with an alphanumeric code (1-4, a-b) above the branch and its respective eigenvalue is represented below the branch. Pseudospecies written in black and in grey are the discriminative indicator and preferential pseudospecies respectively. Superscript numbers in the species abbreviations refer to abundance (IES values) levels understood as pseudospecies: 1- IES = 1–50; 2- IES = 51–150, 3- IES = 151–250, and 4- IES > 250. Indicator and preferential pseudospecies above a branch discriminate the forests shown in the upper posterior branches, whereas those pseudospecies below a branch refer to forests of the lower posterior branches. Three dots “...” indicate that more preferential pseudospecies could be represented.

POcc) in the absence of the above mentioned taxa and by the presence of some facultative epiphytic mosses: *Dicranella heteromalla* (Hedw.) Schimp., *Dicranoweisia cirrata* (Hedw.) Lindb. and *Dicranum scoparium* Hedw. (Fig. 4).

The other half of communities (dendrogram branches with letter *b*) is segregated by some Mediterranean, Oceanic and Mediterranean-Oceanic bryophytes (*Orthotrichum acuminatum* H. Philib., *O. striatum* Hedw. and *Habrodon perpusillus* (De Not.) Lindb. (Fig. 4). They only occur in forests situated within the Mediterranean Region (central Spain and central Portugal) and are divided into four subgroups: i) LVi1 y MT01 with communities discriminated by the presence of *Syntrichia laevipila* Brid. and a certain abundance of *Orthotrichum tenellum* Bruch ex Brid. plus the absence or scarcity of *Hypnum cupressiforme*, *Leptodon smithii* and *Radula complanata*, which in turn occur in abundance in the other three subgroups; ii) MT02 and Gre2 have communities distinguished by the abundance of *Habrodon perpusillus* and the lack of *Alleniella complanata* (Hedw.) S. Olsson, Enroth & D. Quandt; iii) Gre1 and Est1 include *A. complanata* and diverge from the next subgroup by the occurrence of *Cryphaea heteromalla* (Hedw.) D. Mohr, *Homalothecium sericeum* (Hedw.) Schimp. and *Nogopterium gracile* (Hedw.) Crosby & W.R. Buck; iv) LVi2 mainly differs from the previous community by the presence of *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen, *Leucodon sciurooides* (Hedw.) Schwägr and *Orthotrichum pallens* Bruch ex Brid. (Fig. 4).

Direct gradient analysis CCA

The CCA ordination plot (Fig. 5) shows a significant model (first axis $p < 0.01$ and all axis $p < 0.01$) with three explanatory variables: mean summer temperatures (T_{sum}), mean annual rainfall (P) and altitude. The eigenvalues are 0.38 and 0.20 for the first and second axis respectively.

Along the first axis, the communities on trunks of forests MTo1, MTo2, LVi1, LVi2, Gre1 and Gre2 appear in the left side of the ordination plot, characterised by the high mean summer temperatures (T_{sum}) of the localities where they live, and the relevance of the Mediterranean, Mediterranean-Oceanic and Oceanic phytogeographical elements. Most of these communities harbour in abundance the liverworts *Frullania dilatata* and *Metzgeria furcata* and the mosses *Habrodon perpusillus* and *Leptodon smithii* (Fig. 5, Table 3). They also share moderate IES values of *Leucodon sciuroides* and several *Orthotrichum* species (*O. acuminatum*, *O. lyellii*, *O. striatum* and *O. tenellum*) (Fig. 5, Table 3). At the right side of the ordination plot (Fig. 5) we find the forests sampled within the Eurosiberian Region, CCan, Gere and POcc, plus the transitional forest Anca. They are discriminated by the mean annual rainfall (P), the Eurosiberian-Oceanic and Eurosiberian phytogeographical elements, and the importance of the liverwort *Frullania tamarisci* together with the mosses *Hypnum andoi* A.J.E. Sm., *Isothecium myosuroides* and *Neckera pumila* Hedw. However, these forests do not share a common floristic assemblage. Gere is discriminated by the presence of *Harpalejeunea molleri* (Steph.) Grolle whereas CCan and POcc forests diverge by moderate values of *Microlejeunea ulicina* and *Frullania fragilifolia* and the exclusive participation of *Ulota calvescens* Wilson (Fig. 5, Table 3). The Mediterranean forests Aço1 and Aço2 and the transitional forests Mon1 and Mon2, appear close to the centre of the plot as a result of the intermediate nature of their bryophyte community composition (Table 3, Fig. 5). Most of these forests share *Frullania tamarisci* with all those forests located within the Eurosiberian Region as well as harbour *Orthotrichum* species that co-occur in the rest of the forests within the Mediterranean Region (Table 3, Fig. 5). Furthermore, Aço1, Aço2, Mon1 and Mon2 hold common species across almost all the studied forests like *Radula complanata* and *Hypnum cupressiforme* (Table 3, Fig. 5).

Samples and species dispersion regarding the second axis are mainly related to altitude (Fig. 5). Lower sectors of the plot include all the communities sampled at lower altitudes, 625 m or less, (CCan, POcc, Mon2, LVi2, Aço1 and Aço2) but also Anca at 740 m. Most of these forests share *Alleniella complanata* and show high scores of the Indifferent element due to high IES valued of *Hypnum cupressiforme* (Table 3, Fig. 5). Upper sectors of the plot comprise most of the forests living above 620 m (Gre2, Gre1, LVi1, Mon1, MTo1, MTo2, and Gere). At the upper right sector, the community from Gere arises with great abundances of *Frullania tamarisci* and *Hypnum andoi* whereas MTo2, Gre1 and Gre2 occur slightly segregated in the upper left sector where *Habrodon perpusillus*, *Leptodon smithii* and *Orthotrichum rupestre* Schleich. ex Schwägr stand out (Fig. 5 and Table 3). Some forests at the highest altitudes from different biogeographical regions (e.g. MTo2 and Gere) share species like *Porella obtusata* (Fig. 5 and Table 3).

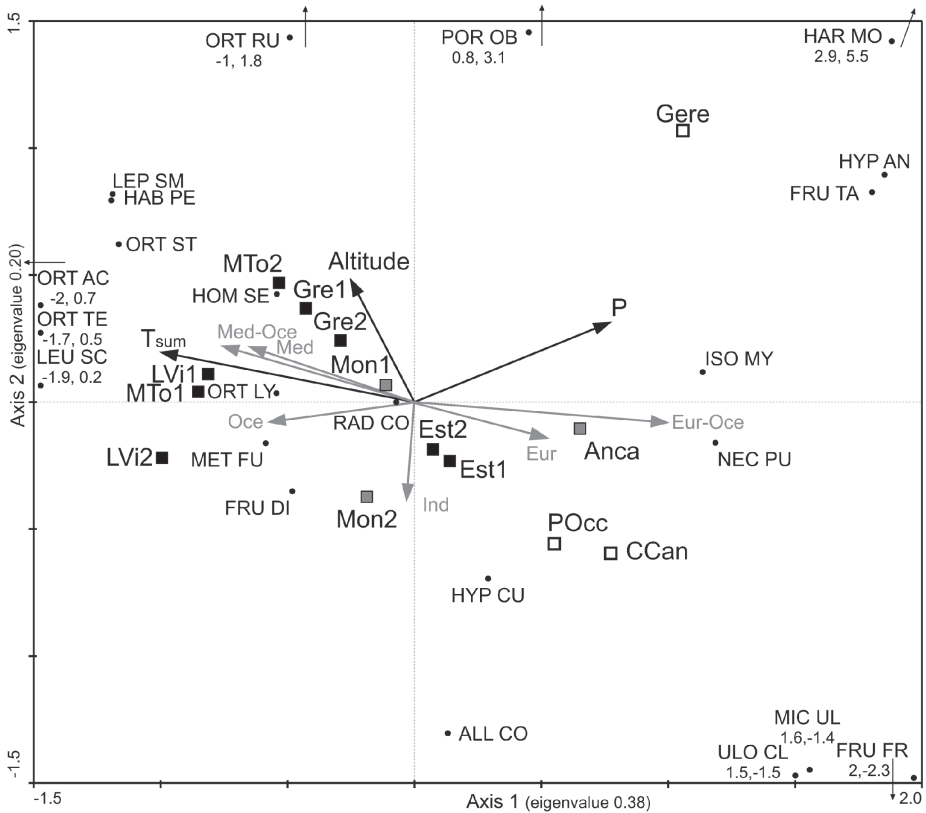


Fig. 5. Canonical correspondence analysis (CCA) plot of the epiphytic bryophyte communities from *Prunus lusitanica* forests. Populations are shown in quadrats: black = Mediterranean Region, white = Eurosiberian Region, grey = transitional between both regions. Significant environmental variables are shown in black arrows. P = mean annual rainfall, T_{sum} = mean summer temperature (June to August). Phytogeographical elements are shown with grey arrows as supplementary variables: Eur = Eurosiberian, Eur-Oce = Eurosiberian-Oceanic, Ind = Indifferent, Med = Mediterranean, Med-Oce = Mediterranean-Oceanic, Oce = Oceanic. Only species with weights greater than 5% are represented (black dots). When the optimum of a species is outside the plot, its coordinates (axis 1, axis 2) are represented under its name and a thin arrow accompanies its label. Full names of forests and species are provided in Tables 1 and 3.

DISCUSSION

Richness and diversity

The total epiphytic bryophyte richness on trunks of *Prunus lusitanica* (53 species) is greater than that of other singular Iberian forests (always excluding the tree base and branches), particularly those dominated by *Juniperus thurifera* (44 species) (Medina *et al.*, 2010), *Abies pinsapo* (23 taxa) (Guerra, 1982) or *Rhododendron ponticum* subsp. *baeticum* (31 species) (Guerra *et al.*, 2003). Compared to *A. pinsapo* or *R. ponticum* forests, *Prunus lusitanica* groves are more widely distributed and their epiphytic communities could be enriched with the floristic pools related to different climatic and biogeographical regions (Medina *et*

al., 2014). Conversely, *Juniperus thurifera* forests have been studied throughout a large geographic range but they are affected by a relatively homogeneous and harsh Mediterranean, relatively dry and continental climate that constrains their total epiphyte richness (Medina *et al.*, 2010).

Some typical Mediterranean and Submediterranean oak forests widespread in the Iberian Peninsula exhibit similar or even lower richness figures than those of *P. lusitanica* forests. Recent studies from a wide area of northwestern Spain (Medina *et al.*, 2015) render 40 species for *Quercus faginea* Lam. forests and up to 66 species for *Q. ilex* subsp. *ballota* forests. This last type of woodlands holds over 50 taxa in Portugal (Garcia, 2006) and in a few localities from southern Spain (Guerra, 1982; Mazimpaka *et al.*, 2009). In wetter regions from northern and central Spain, Submediterranean forests dominated by *Fagus sylvatica* L. or *Quercus pyrenaica* Willd. also hold less than 50 species (Lara, 1993; Burgaz *et al.*, 1994a, 1994b; Garcia, 2006). Only an exhaustive study focused on northwestern Atlantic and Subatlantic oak forests (of *Q. robur* L. and *Q. pyrenaica*), including very wet regions, shows a greater richness, 74 species, the highest species diversity recorded in the Iberian Peninsula (Albertos *et al.*, 2005).

Epiphytic bryophyte richness in the studied *Prunus lusitanica* forests varies from 11 to 20 species (mean = 16.4), without noticeable differences among forests located in the Mediterranean (mean = 16.0 species) and Eurosiberian Regions or its boundaries (mean = 17.0 species). Likewise, diversity values remain almost constant in most forests ($H' = 2.0$ - 2.5 , except for Mon1 where $H' = 1.7$) yet species composition varies widely across the Iberian Peninsula. Other Iberian forests support similar richness figures per forest (Mazimpaka *et al.*, 2009 and references therein) and harbour either relatively homogeneous communities (Medina *et al.*, 2010) or gradual floristic variations (Lara, 1993; Albertos, 2001; Garcia, 2006).

In *Prunus lusitanica* forests, the family *Orthotrichaceae* stands out thanks to the genus *Orthotrichum* (with 11 species) as described for many other Iberian (Lara & Mazimpaka, 1994; Lara *et al.*, 1997; Marques *et al.*, 2005; Medina *et al.*, 2010) and North African epiphytic communities (Draper *et al.*, 2006, 2008). However, *Orthotrichum* species are photophilous and hardly thrive in the typical shady environments of *P. lusitanica* forests. Sampled *Orthotrichum* specimens often lacked sporophytes and showed a depauperate aspect. Most *Orthotrichum* species showed low abundance values and occurred in a low number of forests, being relatively common in some Mediterranean localities. Only *O. lyellii* grows in most of the surveyed forests. Instead, epiphytic communities of *P. lusitanica* groves are quantitatively governed by scio-hygrophilous taxa amongst which the liverwort families Frullaniaceae, Metzgeriaceae and Lejeuneaceae and several pleurocarpous mosses (e.g. *Alleniella complanata*, *Hypnum sp. pl.*, *Isothecium myosuroides* and *Neckera pumila*) stand out. These composition traits agree much of what is recorded in Macaronesian evergreen forests (Patiño *et al.*, 2009; Sim-Sim *et al.*, 2011).

The number of liverwort species hosted by *Prunus lusitanica* forests, 12 in total and 2–8 per forest, exceed those of other Iberian forests (0–5 species) (Gil & Guerra, 1981, 1985; Gil *et al.*, 1985; Burgaz *et al.*, 1994b; Lara & Mazimpaka, 1994; Lara *et al.*, 1997; Marques *et al.*, 2005; Mazimpaka *et al.*, 2009; Medina *et al.*, 2010; Medina *et al.*, 2015). Only woody communities dominated by the relict shrub *Rhododendron ponticum* and some western and northwestern oak forests, have a similar or greater diversity of liverworts (Guerra *et al.*, 2003; Albertos *et al.*, 2005; Garcia, 2006). The *P. lusitanica* forests located in the Eurosiberian Region accommodate more liverwort species than those located in the Mediterranean Region. This trend accords with the drought intolerance of most epiphytic liverworts

(Bischler, 2004). It is noteworthy that *P. lusitanica* forests located in the Mediterranean Region tend to support more liverworts (2–6 species per forest) than most other Mediterranean Iberian forest types (0–4 species per forest) (Guerra, 1982; Burgaz *et al.*, 1994b; Lara & Mazimpaka, 1994; Lara *et al.*, 1997; Mazimpaka *et al.*, 2009; Medina *et al.*, 2010, 2015). These unusual numbers of liverworts may reflect the preferences of *P. lusitanica* for wet habitats (Calleja & Sainz 2009; Pulido *et al.*, 2008). In addition, its evergreen foliage must also favor hygrophilous bryophytes such as liverworts by reducing the detrimental effect of solar irradiance (Song *et al.*, 2014), and hence buffering temperatures and atmospheric humidity changes during dry summers and winters (Silleet & Antoine, 2004; Király *et al.*, 2013).

Biogeographic islands

Prunus lusitanica forests lack typical Macaronesian bryophyte species when compared to forests dominated by another Iberian tertiary relict, *Rhododendron ponticum* (Guerra *et al.*, 2003). Furthermore, in the Eurosiberian Region, *P. lusitanica* forests support epiphytic assemblages co-dominated by Eurosiberian and Oceanic species whereas the Mediterranean elements are poorly represented, as happens in western and northern Iberian forests growing in Atlantic or subAtlantic climatic conditions (Sin-Sim *et al.*, 1995; Albertos, 2001; Albertos *et al.*, 2005). The character of the epiphytic communities spectra of these Eurosiberian *P. lusitanica* forests matches the predominant biogeographical and climate pattern. Thus, *P. lusitanica* forests within the Eurosiberian Region have no meaningful role as biogeographic islands. Conversely, the low significance of the Mediterranean element (0–14.3%) in *P. lusitanica* forests located within the Mediterranean Region (MTo1, MTo2, LVi1, LVi2, Gre1, Gre2, Est1 and Est2) is noteworthy. Here, Oceanic species emerge as dominant or codominant (26.3–40%) along with Mediterranean-Oceanic ones (6.7–31.6%). Epiphytic communities share spectra with a high proportion of species intolerant to prolonged water stress, which usually avoid locations where summer drought lasts for several months (*sensu* Font Tullot, 1983). Similar phylogeographical patterns are found in other Iberian forests affected by exceptionally wet microclimatic conditions (Gil & Guerra, 1981; Guerra *et al.*, 2003; Mazimpaka *et al.*, 2009).

The unusual number of liverwort species might also reflect the singularity of the epiphytic communities growing on *P. lusitanica* trunks in the Mediterranean Region. Epiphytic communities are quantitatively characterised by the abundance (IES values) of three Oceanic and Eurosiberian liverworts (*Frullania dilatata*, *Metzgeria furcata* and *Radula complanata*), co-occurring with hygrophilous and non-Mediterranean liverworts and mosses (e.g. *Cololejeunea minutissima* (Sm.) Schiffn., *Lejeunea cavifolia*, *Neckera pumila*) (Calleja *et al.*, 2014). Likewise, drought-tolerant and shade-sensitive taxa occur at low levels of abundance or are totally absent. Many typical Mediterranean species (within the genera *Grimmia* Hedw., *Hedwigia* P. Beauv., *Orthotrichum*, *Syntrichia* Brid., *Tortula* Hedw., and *Zygodon* Hook. & Taylor) remain unrecorded on *P. lusitanica* trunks whereas they grow as common epiphytes in other Iberian forest types (Lara & Mazimpaka, 1994; Lara *et al.*, 1997; Mazimpaka *et al.*, 2009; Medina *et al.*, 2010, 2015). Thus, *P. lusitanica* forests harbour epiphytic bryophyte communities mainly governed by species that are not typical of the Mediterranean Region, including a high proportion of liverworts even within the Mediterranean Region itself. These findings, together with the existence of other singular, non-epiphytic, hygrophilous bryophytes (Albertos *et al.*, 1997; Casas *et al.*, 1998, 1999; Lara *et al.*, 1999; Sérgio *et al.*, 2001)

reveal the potential role of *P. lusitanica* enclaves as ecological refuges or biogeographic islands within the Mediterranean Region.

Community composition variability

Despite the common phytogeographical traits of epiphytic communities from *Prunus lusitanica* forests, species composition varies markedly across the Iberian Peninsula. This variability is not random but shows general trends mainly modelled by climate, as has been inferred in other studies on epiphytic bryophytes (Sim-Sim *et al.*, 1995; Draper *et al.*, 2006; Garcia, 2006; Medina *et al.*, 2014). In the present study, we found that two climate variables, summer temperatures and mean annual rainfall, significantly correlate with the distribution of some indicator species and phytogeographical elements (Fig. 5).

One group of epiphytic communities lives in Mediterranean areas with high summer temperatures (MTo1, MTo1, LVi1, LVi2, Gre1, Gre2). Such areas support species related to Mediterranean and Oceanic elements with two discriminative *Orthotrichum* species (*O. acuminatum* and *O. striatum*) and noticeable abundances of certain explicative mosses (*Habrodon perpusillus*, *Leptodon smithii* and *Orthotrichum lyellii*) and liverworts (*Metzgeria furcata* and *Frullania dilatata*). The water stress linked to the typical high summer temperatures of the Mediterranean Region might explain the occurrence of some of these species together with typical drought-tolerant species (e.g. *Antitrichia californica* Sull., *Leucodon sciuroides*, *Syntrichia laevipila*). Conversely, another group of epiphytic communities arises in Eurosiberian areas affected by wetter and milder summer climates (Anca, CCan, Gere, POcc). They are successfully discriminated by the liverwort *Frullania tamarisci* along with many other drought-intolerant species (e.g. *Isothecium myosuroides*, *Frullania fragilifolia*, *Ulota sp. pl.*) related to the Eurosiberian-Oceanic and Eurosiberian phytogeographical elements (Table 3).

In addition, we find some *Prunus lusitanica* forests within the western edge of the Mediterranean Region (Aço1 and Aço2) and at its Northeastern border (Mon1 and Mon2), which host communities that share species of both main groups. Both areas are influenced by humidity, originating either from the Atlantic Ocean or from the summer storms of the Gulf of Lyon (Ulbrich *et al.*, 2012), that might favour the occurrence of Eurosiberian-Oceanic species that are also found in *P. lusitanica* forests within the Eurosiberian Region (e.g. *Frullania tamarisci* and *Isothecium myosuroides*). They also share taxa with forests located within the Mediterranean Region (e.g. *Cryphaea heteromalla*, *Homalothecium sericeum*, *Leptodon smithii*, *Orthotrichum sp. pl.*).

Within the resulting two main groups of communities, a noticeable floristic variability can be also partly explained by altitude. Forests located in Mediterranean areas at higher altitudes (e.g. MTo2, at 900 m) incorporate more extra-Mediterranean species or greater levels of abundance of this type of bryophytes (e.g. *Leptodon smithii*, *Neckera pumila*, *Porella obtusata*). Likewise, forests located in the Eurosiberian areas at higher altitudes house communities with high covers of *Hypnum andoi*. However, we still detect an unknown portion of variability in both species composition and species abundances that may be due to unmeasured factors acting at different scales (Raabe *et al.*, 2010; Király *et al.*, 2013; Medina *et al.*, 2014).

CONCLUSIONS

The Iberian forests of *Prunus lusitanica* are remarkably rich in bryophytes. Epiphytic communities are highly heterogeneous, including few species that are widespread in almost all studied groves. Dominance of liverworts and pleurocarpous mosses related to extra-Mediterranean elements characterises the community composition and phytogeographical spectra. These traits enhance the floristic singularity of the Iberian *P. lusitanica* forests and reveal their potential role as biogeographic islands, although this is mainly stressed within the Mediterranean Region.

The great variability, both in species composition and species abundances of the epiphytic bryophyte communities of *Prunus lusitanica* forests can be significantly explained by climate variables. Summer temperatures and annual precipitation seem to determine two main types of communities that fit the principal climates and biogeographical regions of the Iberian Peninsula. These two main types of communities possess their respective differential and characteristic species.

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Appendix 1. Phytogeographical characterisation of epiphytic bryophyte species of *Prunus lusitanica* forests.

<i>Species</i>	<i>Dürl (1983, 1984, 1985, 1992)</i>	<i>Hill & Preston (1998)</i>	<i>Albertos 2001</i>	<i>This work</i>
<i>Alleniella complanata</i>	Temperate	European Boreo-Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Antirrhichia californica</i>	Mediterranean	Mediterranean	Mediterranean	Mediterranean
<i>Antirrhichia curtipendula</i>	Suboceanic	European Boreo-Temperate	Euro Siberian	Euro Siberian
<i>Brachytheciastrum dieckii</i>	—	—	—	Mediterranean Oceanic
<i>Brachytheciastrum velutinum</i>	Temperate	Circumpolar Temperate	Indifferent (Oceanic)	Oceanic
<i>Cololejeunea minutissima</i>	Oceanic-Mediterranean Western	Hyperoceanic Temperate	—	Oceanic
<i>Cololejeunea rossettiana</i>	Submediterranean-montane	Submediterranean Subatlantic	—	Oceanic
<i>Cryphaea heteromalla</i>	Suboceanic-Mediterranean	Submediterranean Subatlantic	Indifferent (Oceanic)	Oceanic
<i>Dicranella heteromalla</i>	Temperate	Circumpolar Boreo-Temperate	—	Euro Siberian Oceanic
<i>Dicranoweisia cirrata</i>	Suboceanic	European Temperate	Indifferent (Oceanic)	Oceanic
<i>Dicranum scoparium</i>	Subboreal	Circumpolar Boreal	Euro Siberian	Euro Siberian
<i>Fabronia pusilla</i>	—	Mediterranean Atlantic	—	Mediterranean Oceanic
<i>Frullania dilatata</i>	Temperate	Euroasiatic Temperate	Indifferent (Oceanic)	Oceanic
<i>Frullania fragifolia</i>	Suboceanic-montane	Suboceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Frullania microphylla</i>	Euoceanic-montane	Hyperoceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Frullania oakesiana</i>	Relictual North Eu-Oceanic	—	—	Oceanic
<i>Frullania tamarisci</i>	Western Temperate-montane	Suboceanic Boreo-Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Grimmia trichophylla</i>	Temperate-montane	Circumpolar	Mediterranean	Mediterranean Oceanic
<i>Habrodon perpusillus</i>	Mediterranean-Oceanic	Mediterranean Atlantic	Mediterranean	Mediterranean Oceanic
<i>Harpalejeunea molleri</i>	Oceanic-Submediterranean	Hyperoceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Homalothecium sericeum</i>	Temperate	Euro Siberian Temperate	Indifferent	Indifferent
<i>Hypnum andoi</i>	Oceanic	Suboceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Hypnum cupressiforme</i>	Temperate (filiiformis: Oceanic)	Circumpolar Temperate	Indifferent	Indifferent
<i>Isoetium alopecuroides</i>	Temperate	European Boreo-Temperate	Euro Siberian	Euro Siberian
<i>Isoetium myosuroides</i>	Suboceanic-(Submediterranean)	Suboceanic Boreo-Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Lejeunea cavifolia</i>	Suboceanic-montane	Boreo Temperate Circumpolar	—	Euro Siberian

<i>Leptodon smithii</i>	Oceanic-Mediterranean	Mediterranean Atlantic	Mediterranean	Mediterranean Oceanic
<i>Leucodon sciuroides</i>	Temperate	Euro Siberian Temperate	Indifferent (Oceanic)	Indifferent
<i>Metzgeria furcata</i>	Western Temperate	European Boreal Temperate	Indifferent (Oceanic)	Oceanic
<i>Microlejeunea ulicina</i>	Suboceanic	Suboceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Neckera pumila</i>	North Suboceanic	Suboceanic Temperate	Euro Siberian	Euro Siberian Oceanic
<i>Nogopterium gracile</i>	Suboceanic-Submediterranean-montane	Submediterranean Subatlantic	Indifferent (Oceanic)	Oceanic
<i>Orthotrichum scanicum</i>	Submediterranean-Suboceanic	—	Mediterranean	Mediterranean
<i>Orthotrichum acuminatum</i>	Submediterranean-montane	Mediterranean	Mediterranean	Mediterranean
<i>Orthotrichum affine</i>	Temperate	European Boreo-Temperate	Indifferent (Oceanic)	Indifferent
<i>Orthotrichum ibericum</i>	—	Mediterranean Atlantic	Mediterranean	Mediterranean Oceanic
<i>Orthotrichum lyellii</i>	Suboceanic-Submediterranean	Suboceanic Temperate	Indifferent (Oceanic)	Oceanic
<i>Orthotrichum pallens</i>	Subboreal montane	Boreo Temperate	—	Euro Siberian
<i>Orthotrichum pumilum</i>	Temperate	European Temperate	Mediterranean	Mediterranean
<i>Orthotrichum rupestre</i>	North Suboceanic-montane	European Boreo-Temperate	Mediterranean	Mediterranean
<i>Orthotrichum speciosum</i>	Subcontinental	Circumpolar Boreo-Arctic montane	Euro Siberian	Euro Siberian
<i>Orthotrichum striatum</i>	Suboceanic	European Boreo-Temperate	Indifferent (Oceanic)	Oceanic
<i>Orthotrichum tenellum</i>	Submediterranean-Suboceanic	Submediterranean Subatlantic	Mediterranean	Mediterranean Oceanic
<i>Porella obtusata</i>	Western Mediterranean-montane	Oceanic Temperate	Indifferent (Oceanic)	Oceanic
<i>Pterigynandrum filiforme</i>	Boreal-montane	Circumpolar Boreal montane	Euro Siberian	Euro Siberian
<i>Radula complanata</i>	Western Temperate	Circumpolar Boreo-Temperate	Indifferent	Euro Siberian
<i>Rhynchostegium confertum</i>	Submediterranean-Oceanic	European Temperate	Indifferent (Oceanic)	Indifferent
<i>Syntrichia laevipila</i>	Oceanic-Submediterranean	Submediterranean Subatlantic	Indifferent (Oceanic)	Mediterranean Oceanic
<i>Ulota bruchii</i>	North Suboceanic	—	Euro Siberian	Euro Siberian
<i>Ulota crispa</i>	Temperate	European Temperate Circumpolar	Euro Siberian	Euro Siberian
<i>Ulota crispula</i>	—	—	—	Euro Siberian
<i>Zygodon rupestris</i>	Suboceanic-Mediterranean	Circumpolar Temperate	Indifferent (Oceanic)	Mediterranean Oceanic

Appendix 2. Complete data of the TWINSPAN analysis

Symbols “+” and “-“ refer to the lower and upper branches respectively of each dichotomy in Fig. 4.

Selected preferential species are shown in bold. Selected preferential species occur in over 80% of forests of one group and in less than 20% of those of the other group of each dichotomy.

Only three species (including indicators) per group are represented in Fig. 4.

QUADRAT DIVISION 1 Number of quadrats in cluster = 14
eigenvalue = 0.3552 number of iterations = 3

Indicators and their sign

ORT AC [+];

ORT ST [+];

Maximum indicator score for the negative group = 0

Minimum indicator score for the positive group = 1

Negative group: 2. Comprised by 7 objects: Gere, Mon1, Anca, Mon2, Ccan, POcc, Est2,

Positive group: 3. Comprised by 7 objects: LVi1, Gre1, Est1, Mto1, Mto2, Gre2, LVi2,

Species preferring the negative group of quadrats:

BRA VE 1 (4, 2) COL MI 1 (2, 1) DIC SC 1 (2, 0) FRU FR 1 (3, 0) FRU MI 1 (2, 0) **FRU TA 1 (6, 1)** HYP AN 1 (3, 1) ISO MY 1 (5, 2) LEJ CA 1 (4, 1) MIC UL 1 (3, 0) ALL CO 1 (6, 3) ORT AF 1 (2, 1) PTE FI 1 (2, 0) ULO BR 1 (2, 0) ULO CR 1 (2, 0) ULO CL 1 (2, 0) ZYG RU 1 (6, 3) FRU FR 2 (2, 0) FRU TA 2 (3, 0) HYP AN 2 (2, 0) ISO MY 2 (4, 0) MIC UL 2 (2, 0) ALL CO 2 (3, 0) FRU TA 3 (3, 0) HYP CU 3 (3, 1) ISO MY 3 (2, 0) NEC PU 3 (4, 1) RAD CO 3 (3, 0) FRU TA 4 (2, 0) NEC PU 4 (4, 1)

Species biased towards the positive group of quadrats:

HAB PE 1 (1, 7) HOM SE 1 (0, 4) LEP SM 1 (3, 6) LEU SC 1 (0, 4) ORT AC 1 (0, 6) ORT RU 1 (1, 3) ORT ST 1 (0, 6) **ORT TE 1 (1, 6)** NOG GR 1 (1, 3) SYN LA 1 (0, 2) **HAB PE 2 (0, 6)** HOM SE 2 (0, 2) LEP SM 2 (0, 4) ORT LY 2 (2, 6) ORT TE 2 (0, 2) HAB PE 3 (0, 2) LEP SM 3 (0, 3)

Species with no quadrat preference:

CRY HE 1 (2, 2) FRU DI 1 (7, 7) HYP CU 1 (7, 7) MET FU 1 (7, 7) NEC PU 1 (5, 3) ORT LY 1 (6, 7) POR OB 1 (3, 3) RAD CO 1 (6, 6) FRU DI 2 (7, 7) HYP CU 2 (6, 4) MET FU 2 (7, 6) NEC PU 2 (5, 3) RAD CO 2 (5, 4) FRU DI 3 (4, 6) MET FU 3 (5, 5) FRU DI 4 (3, 4) MET FU 4 (3, 5)

END OF LEVEL 1

QUADRAT DIVISION 2a Number of quadrats in cluster = 7
eigenvalue = 0.4084 number of iterations = 4

Indicators and their sign

ISO MY [+];

Maximum indicator score for the negative group = 0

Minimum indicator score for the positive group = 1

Negative group: 4. Comprised by 2 objects: Mon1, Mon2,

Positive group: 5. Comprised by 5 objects: Gere, Anca, Ccan, POcc, Est2,

Species preferring the negative group of quadrats:

COL MI 1 (1, 1) COL ROS 1 (1, 0) CRY HE 1 (1, 1) EUR 1 (1, 0) LEJ CA 1 (2, 2) ORT SC 1 (1, 0) **ORT AF 1 (2, 0)** ORT PU 1 (1, 0) ORT TE 1 (1, 0) RHY CO 1 (1, 0) BRA VE 2 (1, 0) COL ROS 2 (1, 0) LEJ CA 2 (1, 0) ALL CO 3 (1, 0) RAD CO 3 (2, 1) MET FU 4 (2, 1) RAD CO 4 (1, 0)

Species biased towards the positive group of quadrats:

DIC SC 1 (0, 2) FRU FR 1 (0, 3) FRU MI 1 (0, 2) FRU TA 1 (1, 5) HYP AN 1 (0, 3) ISO MY 1 (0, 5) **NEC PU 1 (0, 5)** PTE FI 1 (0, 2) ULO BR 1 (0, 2) ULO CR 1 (0, 2) ULO CL 1 (0, 2) FRU FR 2 (0, 2) FRU TA 2 (0, 3) HYP AN 2 (0, 2) **ISO MY 2 (0, 4)** MIC UL 2 (0, 2) **NEC PU 2 (0, 5)** ORT LY 2 (0, 2) FRU TA 3 (0, 3) HYP CU 3 (0, 3) ISO MY 3 (0, 2) **NEC PU 3 (0, 4)** FRU TA 4 (0, 2) **NEC PU 4 (0, 4)**

Species with no quadrat preference:

BRA VE 1 (1, 3) FRU DI 1 (2, 5) HYP CU 1 (2, 5) LEP SM 1 (1, 2) MET FU 1 (2, 5) MIC UL 1 (1, 2) ALL CO 1 (2, 4) ORT LY 1 (2, 4) POR OB 1 (1, 2) RAD CO 1 (2, 4) ZYG RU 1 (2, 4) FRU DI 2 (2, 5) HYP CU 2 (2, 4) MET FU 2 (2, 5) ALL CO 2 (1, 2) RAD CO 2 (2, 3) FRU DI 3 (1, 3) MET FU 3 (2, 3) FRU DI 4 (1, 2)

QUADRAT DIVISION 2b Number of quadrats in cluster = 7

eigenvalue = 0.331 number of iterations = 2

Indicators and their sign

SYN LA [+];

Maximum indicator score for the negative group = 0

Minimum indicator score for the positive group = 1

Negative group: 6. Comprised by 5 objects: Gre1, Est1, Mto2, Gre2, LVi2,

Positive group: 7. Comprised by 2 objects: LVi1, Mto1,

Species preferring the negative group of quadrats:

CRY HE 1 (2, 0) LEP SM 1 (5, 1) ALL CO 1 (3, 0) NEC PU 1 (3, 0) ORT RU 1 (3, 0) POR OB 1 (3, 0) RAD CO 1 (5, 1) HAB PE 2 (5, 1) HOM SE 2 (2, 0) **HYP CU 2 (4, 0)** **LEP SM 2 (4, 0)** NEC PU 2 (3, 0) **RAD CO 2 (4, 0)** HAB PE 3 (2, 0) LEP SM 3 (3, 0)

Species biased towards the positive group of quadrats:

ANT CA 1 (0, 1) BRA DI 1 (0, 1) BRA VE 1 (1, 1) GRI TR 1 (0, 1) HOM SE 1 (2, 2) HYP AN 1 (0, 1) ISO MY 1 (1, 1) LEJ CA 1 (0, 1) ORT AF 1 (0, 1) ORT SP 1 (0, 1) SYN LA 1 (0, 2) ORT AC 2 (0, 1) **ORT TE 2 (0, 2)** ORT LY 3 (0, 1) ORT TE 3 (0, 1) FRU DI 4 (2, 2)

Species with no quadrat preference:

FRU DI 1 (5, 2) HAB PE 1 (5, 2) HYP CU 1 (5, 2) LEU SC 1 (3, 1) MET FU 1 (5, 2) ORT AC 1 (4, 2) ORT LY 1 (5, 2) ORT ST 1 (4, 2) ORT TE 1 (4, 2) NOG GR 1 (2, 1) ZYG RU 1 (2, 1) FRU DI 2 (5, 2) MET FU 2 (4, 2) ORT LY 2 (4, 2) FRU DI 3 (4, 2) MET FU 3 (4, 1) MET FU 4 (4, 1)

END OF LEVEL 2

QUADRAT DIVISION 3a Number of quadrats in cluster = 5

eigenvalue = 0.3783 number of iterations = 1

Indicators and their sign

FRU FR [+];

Maximum indicator score for the negative group = 0

Minimum indicator score for the positive group = 1

Negative group: 10. Comprised by 2 objects: Gere, Est2,

Positive group: 11. Comprised by 3 objects: Anca, Ccan, POcc,

Species preferring the negative group of quadrats:

ANT CU 1 (1, 0) COL MI 1 (1, 0) CRY HE 1 (1, 0) HAR MO 1 (1, 0) ISO AL 1 (1, 0) **LEJ CA 1 (2, 0)** ORT RU 1 (1, 0) **POR OB 1 (2, 0)** NOG GR 1 (1, 0) FRU TA 2 (2, 1) HAR

MO 2 (1, 0) POR OB 2 (1, 0) NOG GR 2 (1, 0) RAD CO 2 (2, 1) ZYG RU 2 (1, 0) FRU TA 3 (2, 1) **ISO MY 3 (2, 0)** POR OB 3 (1, 0) RAD CO 3 (1, 0) ISO MY 4 (1, 0)

Species biased towards the positive group of quadrats:

DIC HE 1 (0, 1) DIC CI 1 (0, 1) FRU FR 1 (0, 3) FRU MI 1 (0, 2) FRU OAK 1 (0, 1) HAB PE 1 (0, 1) LEP SM 1 (0, 2) MIC UL 1 (0, 2) ULO BR 1 (0, 2) ULO CR 1 (0, 2) ULO CL 1 (0, 2) FRU FR 2 (0, 2) HYP CU 2 (1, 3) MIC UL 2 (0, 2) ORT LY 2 (0, 2) ULO CL 2 (0, 1) HYP AN 3 (0, 1) **HYP CU 3 (0, 3)** ORT LY 3 (0, 1) HYP AN 4 (0, 1) MET FU 4 (0, 1)

Species with no quadrat preference:

BRA VE 1 (1, 2) DIC SC 1 (1, 1) FRU DI 1 (2, 3) FRU TA 1 (2, 3) HYP AN 1 (1, 2) HYP CU 1 (2, 3) ISO MY 1 (2, 3) MET FU 1 (2, 3) ALL CO 1 (2, 2) NEC PU 1 (2, 3) ORT LY 1 (2, 2) PTE FI 1 (1, 1) RAD CO 1 (2, 2) ZYG RU 1 (2, 2) FRU DI 2 (2, 3) HYP AN 2 (1, 1) ISO MY 2 (2, 2) MET FU 2 (2, 3) ALL CO 2 (1, 1) NEC PU 2 (2, 3) FRU DI 3 (1, 2) MET FU 3 (1, 2) NEC PU 3 (2, 2) FRU DI 4 (1, 1) FRU TA 4 (1, 1) NEC PU 4 (2, 2)

QUADRAT DIVISION 3b Number of quadrats in cluster = 5

eigenvalue = 0.3096 number of iterations = 1

Indicators and their sign

ALL CO [-];

Maximum indicator score for the negative group = -1

Minimum indicator score for the positive group = 0

Negative group: 12. Comprised by 3 objects: Gre1, Est1, LVi2,

Positive group: 13. Comprised by 2 objects: Mto2, Gre2,

Species preferring the negative group of quadrats:

BRA VE 1 (1, 0) COL MI 1 (1, 0) CRY HE 1 (2, 0) FAB PU 1 (1, 0) FRU TA 1 (1, 0) HOM SE 1 (2, 0) ISO AL 1 (1, 0) ISO MY 1 (1, 0) ALL CO 1 (3, 0) ORT AC 1 (3, 1) ORT IB 1 (1, 0) ORT PA 1 (1, 0) ORT TE 1 (3, 1) NOG GR 1 (2, 0) ZYG RU 1 (2, 0) CRY HE 2 (1, 0) HOM SE 2 (2, 0) LEU SC 2 (1, 0) MET FU 2 (3, 1) ORT ST 2 (1, 0) NOG GR 2 (1, 0) RAD CO 2 (3, 1) FRU DI 3 (3, 1) MET FU 3 (3, 1) FRU DI 4 (2, 0) MET FU 4 (3, 1)

Species biased towards the positive group of quadrats:

LEU SC 1 (1, 2) NEC PU 1 (1, 2) ORT RU 1 (1, 2) NEC PU 2 (1, 2) ORT RU 2 (0, 1) POR OB 2 (0, 1) **HAB PE 3 (0, 2)** HYP CU 3 (0, 1) LEP SM 3 (1, 2) NEC PU 3 (0, 1) HAB PE 4 (0, 1) LEP SM 4 (0, 1) NEC PU 4 (0, 1)

Species with no quadrat preference:

FRU DI 1 (3, 2) HAB PE 1 (3, 2) HYP CU 1 (3, 2) LEP SM 1 (3, 2) MET FU 1 (3, 2) ORT LY 1 (3, 2) ORT ST 1 (2, 2) POR OB 1 (2, 1) RAD CO 1 (3, 2) FRU DI 2 (3, 2) HAB PE 2 (3, 2) HYP CU 2 (2, 2) LEP SM 2 (2, 2) ORT LY 2 (2, 2)

END OF LEVEL 3

QUADRAT DIVISION 4a Number of quadrats in cluster = 3

eigenvalue = 0.3904 number of iterations = 11

Indicators and their sign

DIC HE [+];

Maximum indicator score for the negative group = 0

Minimum indicator score for the positive group = 1

Negative group: 22 Number of objects = 2 comprising: Ccan, POcc,

Positive group: 23. Comprised by 1 object: Anca,

Species preferring the negative group of quadrats:

FRU OAK 1 (1, 0) **LEP SM 1 (2, 0)** **MIC UL 1 (2, 0)** **ULO BR 1 (2, 0)** **ULO CR 1 (2, 0)**
ULO CL 1 (2, 0) **ORT LY 1 (2, 0)** FRU TA 2 (1, 0) **MIC UL 2 (2, 0)** ALL CO 2 (1, 0)
ORT LY 2 (2, 0) RAD CO 2 (1, 0) ULO CL 2 (1, 0) **FRU DI 3 (2, 0)** FRU TA 3 (1, 0)
MET FU 3 (2, 0) **NEC PU 3 (2, 0)** ORT LY 3 (1, 0) FRU DI 4 (1, 0) FRU TA 4 (1, 0) MET
 FU 4 (1, 0) **NEC PU 4 (2, 0)**

Species biased towards the positive group of quadrats:

BRA VE 1 (1, 1) **DIC HE 1 (0, 1)** **DIC CI 1 (0, 1)** **DIC SC 1 (0, 1)** FRU MI 1 (1, 1) **HAB
 PE 1 (0, 1)** HYP AN 1 (1, 1) ALL CO 1 (1, 1) **PTE FI 1 (0, 1)** RAD CO 1 (1, 1) ZYG RU
 1 (1, 1) FRU FR 2 (1, 1) HYP AN 2 (0, 1) ISO MY 2 (1, 1) **HYP AN 3 (0, 1)** **HYP AN 4
 (0, 1)**

Species with no quadrat preference:

FRU DI 1 (2, 1) FRU FR 1 (2, 1) FRU TA 1 (2, 1) HYP CU 1 (2, 1) ISO MY 1 (2, 1) MET
 FU 1 (2, 1) NEC PU 1 (2, 1) FRU DI 2 (2, 1) HYP CU 2 (2, 1) MET FU 2 (2, 1) NEC PU
 2 (2, 1) HYP CU 3 (2, 1)

QUADRAT DIVISION 4b Number of quadrats in cluster = 3
 eigenvalue = 0.2902 number of iterations = 29

Indicators and their sign

BRA VE [-];

Maximum indicator score for the negative group = -1

Minimum indicator score for the positive group = 0

Negative group: 24. Comprised by 1 object: LVi2,

Positive group: 25. Comprised by 2 objects: Gre1, Est1,

Species preferring the negative group of quadrats

BRA VE 1 (1, 0) **LEU SC 1 (1, 0)** **ORT PA 1 (1, 0)** POR OB 1 (1, 1) LEP SM 2 (1, 1)
LEU SC 2 (1, 0) **LEP SM 3 (1, 0)** FRU DI 4 (1, 1)

Species biased towards the positive group of quadrats:

COL MI 1 (0, 1) **CRY HE 1 (0, 2)** FAB PU 1 (0, 1) FRU TA 1 (0, 1) **HOM SE 1 (0, 2)** ISO
 AL 1 (0, 1) ISO MY 1 (0, 1) NEC PU 1 (0, 1) **NOG GR 1 (0, 2)** ORT IB 1 (0, 1) ORT RU
 1 (0, 1) **ORT ST 1 (0, 2)** **ZYG RU 1 (0, 2)** CRY HE 2 (0, 1) **HOM SE 2 (0, 2)** **HYP CU
 2 (0, 2)** NEC PU 2 (0, 1) **ORT LY 2 (0, 2)** ORT ST 2 (0, 1) NOG GR 2 (0, 1)

Species with no quadrat preference:

FRU DI 1 (1, 2) HAB PE 1 (1, 2) HYP CU 1 (1, 2) LEP SM 1 (1, 2) MET FU 1 (1, 2) ALL
 CO 1 (1, 2) ORT AC 1 (1, 2) ORT LY 1 (1, 2) ORT TE 1 (1, 2) RAD CO 1 (1, 2) FRU DI
 2 (1, 2) HAB PE 2 (1, 2) MET FU 2 (1, 2) RAD CO 2 (1, 2) FRU DI 3 (1, 2) MET FU 3
 (1, 2) MET FU 4 (1, 2)

END OF LEVEL 4

Appendix 3. Environmental variables and supplementary variables used in the Canonical Correspondence Analysis (CCA) of the epiphytic bryoflora of *Prunus lusitanica* forests. Pop = population, Alt (m) = altitude, K = Gorezynski 's Continentiality Index (Aguiló Alonso *et al.* 1995), P = mean annual rainfall, P_{sum} = mean rainfall from June to August, D = Distance of each forest from the sea, T = mean annual temperature, T_{sum} = mean summer temperature (June to August), T_{max} = mean maximum temperature of the hottest month, T_{min} = mean minimum temperature of the coldest month, T_{range} = mean temperature range, Th = annual potential evapotranspiration; Th_{sum} = potential evapotranspiration in summer (June to August). Supplementary variables are the sum of the ISE values of the species grouped into six phytogeographical elements: Eur = Eurosiberian, Eur-Oce = Eurosiberian and Oceanic, Ind = Indifferent, Med = Mediterranean, Med-Oce = Mediterranean and Oceanic, Oce = Oceanic. Evapotranspiration was measured using Thornthwaite 's formula (Aguiló *et al.* 1995).

Pop	Alt (m)	Environmental Variables										Supplementary Variables (ISE)						
		K	P	P _{est}	D	T	T _{sum}	T _{max}	T _{min}	T _{range}	Th	Th _{sum}	Eur	Eur-Oce	Oce	Ind	MedOce	Med
MTol	700	32.9	708.1	61.5	270.3	13.8	23.1	33	0.4	19.9	761.0	406.9	8	0	732	126	176	136
MTol2	900	31.4	651.7	61.4	289.8	12.9	22.1	31.8	0	19.4	727.9	387.5	23	141	925	214	459	134
LVi1	620	31.7	945.4	52.6	276.0	14.2	23.3	32.9	1.2	19.5	775.4	409.7	20	24	985	85	159	39
LVi2	500	31.1	803.0	52.8	269.6	14.6	23.6	33.1	1.8	19.3	792.3	417.1	81	8	758	94	344	21
Gre1	660	28.9	1307.3	76.6	329.1	13.4	22.2	31.3	0.8	18.7	744.9	389.0	93	7	1007	209	270	39
Gre2	630	28.3	1317.9	81.0	327.0	13.1	21.8	31	0.6	18.5	734.4	382.9	128	256	258	128	706	28
Est1	600	18.6	1105.9	71.7	92.0	13.0	19.8	27.1	3	14.8	711.6	339.1	261	70	772	57	43	0
Est2	625	18.0	1048.7	77.8	85.1	13.1	19.9	27.2	3.2	14.6	714.7	339.6	350	252	606	126	24	20
Mon1	760	18.1	887.0	282.0	23.9	11.5	20.6	24.7	0.5	15.4	729.4	354.1	144	141	1015	209	161	6
Mon2	550	18.8	910.4	178.9	27.9	13.4	20.6	25.8	3.1	15.4	729.4	354.1	208	1008	565	70	55	0
Anca	740	16.9	1138.5	111.7	77.1	10.9	17.9	25.4	0.1	14.9	658.0	318.9	30	715	230	220	18	0
Gere	720	13.3	2550.2	209.8	55.0	12.4	18.6	25.4	2.6	13.2	692.8	319.6	203	1192	467	11	11	8
CCan	500	10.2	1247.6	185.0	25.7	11.7	17.2	22.5	3.1	12.3	671.6	302.1	160	1176	752	202	30	0
POce	175	13.1	1921.6	294.6	27.7	12.6	18.7	24.6	2.2	13.5	701.6	324.0	122	683	486	244	8	0

Appendix 4. Canonical Correspondence Analysis (CCA) output data using the statistical package Canoco for Windows 4.5 (Ter Braak & Prentice, 1988; Ter Braak & Smilauer, 2002).

Program CANOCO Version 4.52 October 2003 - written by C.J.F. Ter Braak (C) 1988-2003 - *Biometris - quantitative methods in the life and earth sciences*. Plant Research International, Wageningen University and Research Centre Box 100, 6700 AC Wageningen, the Netherlands.

CANOCO performs (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis. CANOCO is an extension of Cornell Ecology program DECORANA (Hill, 1979).

For explanation of the input/output see the manual or Ter Braak C.J.F. (1995) - *Ordination*. Chapter 5. In: Jongman R.H.G., Ter Braak C.J.F. & Van Tongeren O.F.R. (eds.), *Data Analysis in Community and Landscape Ecology*. Cambridge, UK, Cambridge University Press, 91-173 pp.

*** Type of analysis ***

Model	Gradient analysis		
	indirect	direct	hybrid
linear	1=PCA	2= RDA	3
unimodal	4= CA	5= CCA	6
„	7=DCA	8=DCCA	9
		10=non-standard analysis	

Type analysis number: **Answer = 5**

*** **Data files** ***

Species data C:\Users\pc\Documents\Artículos\Brioflora epifita loreras ibericas\Análisis\Análisis multivariantes \Species Matrix

Environmental data : C:\Users\pc\Documents\Artículos\Brioflora epifita loreras ibericas\Análisis\Análisis multivariantes \Env variables 2015

Initialization file:

Forward selection of envi. variables = 0
 Scaling of ordination scores = 1
 Diagnostics = 3

File: C:\Users\pc\Documents\Artículos\Brioflora epifita loreras ibericas\Análisis\Análisis multivariantes exploratorios\Species Matrix

Format : (I5,I1X,I0F7.1,5/(6X,(I0F7.1)))

No. of couplets of species number and abundance per line: 0

No. of samples omitted 0

Number of samples 14

Number of species 53

Number of occurrences 229

File: C:\Users\pc\Documents\Artículos\Brioflora epifita loreras ibericas\Análisis\Análisis multivariantes exploratorios\Env variables 2015

Format : (I5,I1X,5(I6,F8.1))

No. of environmental variables: 18

No interaction terms defined

No transformation of species data

No species-weights specified (10% per graphic representation)

No sample-weights specified

No downweighting of rare species

No. of active samples: 14

No. of passive samples: 0

No. of active species: 53

Total inertia in species data=

Sum of all eigenvalues of CA = 1.85983

***** Check on influence in covariable/environment data *****

The following sample(s) have extreme values

Sample Environmental Covariable + Environment space

	variable	Influence	influence	influence
11	3	9.7x		
11			3.1x	
14	1	6.2x		

***** End of check *****

**** Weighted correlation matrix (weight = sample total) ****

P = mean annual precipitation; T_sum = Mean temperature from June to August.

SPEC AX1	1.0000										
SPEC AX2	0.0038	1.0000									
SPEC AX3	-0.1101	0.0128	1.0000								
SPEC AX4	0.0299	-0.1153	-0.2505	1.0000							
ENVI AX1	0.9426	0.0000	0.0000	0.0000	1.0000						
ENVI AX2	0.0000	0.9587	0.0000	0.0000	0.0000	1.0000					
ENVI AX3	0.0000	0.0000	0.7358	0.0000	0.0000	0.0000	1.0000				
ENVI AX4	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000			
ALTITUDE	-0.2046	0.6326	-0.5293	0.0000	-0.2171	0.6599	-0.7193	0.0000	1.0000		
P	0.6966	0.3691	0.4068	0.0000	0.7390	0.3850	0.5528	0.0000	-0.3041	1.0000	
T_SUM	-0.8967	0.2738	0.0853	0.0000	-0.9513	0.2856	0.1159	0.0000	0.3116	-0.5290	1.0000

SPEC AX1 SPEC AX2 SPEC AX3 SPEC AX4 ENVI AX1 ENVI AX2 ENVI AX3 ENVI AX4 ALTITUDE P T_SUM

N	name	(weighted) mean	stand. dev.	inflation factor
1	SPEC AX1	0.0000	0.6587	
2	SPEC AX2	0.0000	0.4642	
3	SPEC AX3	0.0000	0.3930	
4	SPEC AX4	0.0000	0.5233	
5	ENVI AX1	0.0000	0.6209	
6	ENVI AX2	0.0000	0.4450	
7	ENVI AX3	0.0000	0.2891	
8	ENVI AX4	0.0000	0.0000	
1	ALTITUDE	605.9386	167.0879	1.1416
3	P	1216.4676	511.0645	1.4313
6	T_SUM	20.4677	2.0211	1.4386

**** Summary ****

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.386	0.198	0.084	0.274	1.860
Species-environment correlations:	0.943	0.959	0.736	0.000	
Cumulative percentage variance					
of species data:	20.7	31.4	35.9	50.6	
of species-environment relation:	57.8	87.5	100.0	0.0	
Sum of all eigenvalues					1.860
Sum of all canonical eigenvalues					0.667

The first three eigenvalues reported above are canonical, the fourth is not since only three independent constraints can be formed from the environmental variables.

*** Unrestricted permutation ***

Seeds: 22456 4053

**** Summary of Monte Carlo test ****

Test of significance of first canonical axis: eigenvalue = 0.386

F-ratio = 2.615

P-value = 0.0020

Test of significance of all canonical axes: Trace = 0.667

F-ratio = 1.864

P-value = 0.0020

(499 permutations under reduced model)